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Spaces of the Possible: Universal Darwinism and the wall between technological and biological innovation

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Abstract

Innovations in biological evolution and in technology have many common features. Some of them involve similar processes, such as trial-and-error and horizontal information transfer. Others describe analogous outcomes, such as multiple independent origins of similar innovations. Yet others display similar temporal patterns, such as episodic bursts of change separated by periods of stasis. We review nine such commonalities, and propose that the mathematical concept of a space of innovations, discoveries, or designs can help explain them. This concept can also help demolish a persistent conceptual wall between technological and biological innovation.

1 **Introduction**

2
3 For thousands of years the western intellectual traditions, whether dated from the pre-
4 Socratics or the first chapters of Genesis have maintained a conceptual wall that separates
5 the world of nature from that of man. But during the last two centuries, a countervailing
6 view emerged. Its roots go back at least to Charles Darwin's *Origin of Species* in 1859.
7 This Darwinian world view began to erase the distinction between human life and the rest
8 of the natural world, and has diffused into nearly every corner of human activity. It gave
9 rise to "universal Darwinism", the application of Darwinian thinking to fields as different
10 as psychology, linguistics, economics, computer science, chemistry, engineering, and
11 cosmology (Campbell 1960; Dawkins 1983; Nelson & Winter 1985; Plotkin 1997;
12 Smolin 1997). The points of contact between Darwinism and other disciplines are usually
13 limited, often not extending beyond some form of "selection". But for one distinctly
14 human activity – technological innovation – they reflect almost everything we have
15 learned about biological evolution in the two centuries since Darwin. Each of the next
16 nine sections reviews a broad commonality between innovation in nature, on the one
17 hand, and in technology and science, on the other. (These commonalities have been
18 explored by many writers cited throughout, but in separate and book-length treatments,
19 not in a concise overview.) The final section ten discusses the causes of these
20 commonalities. Some of them are simple, others quite complex. Taken together, they
21 hint at a deeper principle of *innovability* that emerges from a space of possible
22 innovations that are independent of the history of life or technology (Wagner 2011). The
23 recognition that such a space is universally important for innovation can help erode the
24 conceptual wall between innovations in technology and nature.

25 26 1. Trial-and-Error within populations

27
28 Few readers will be surprised that Nature innovates through trial-and-error, or, as it is
29 sometimes called, trial-and-success (Vermeij 2010). Mutations that range from random
30 changes in individual nucleotides – the four chemical "letters" of DNA – to deletions and
31 duplications of entire genes, and large-scale rearrangements of millions of nucleotides are

1 inevitable by-products of imperfect DNA replication and repair. Many such alterations
2 change an organism's phenotype – its visible or measurable features – and produce a
3 living experiment, a trail that can fail.

4
5 In the eyes of many, human innovation is fundamentally different. Humans have goals.
6 Nature does not. Biological trials lack direction, whereas technological experimentation
7 is highly directional, aimed at solving specific problems.

8
9 The distinction is important, but it hides a more fundamental similarity. The *process* that
10 leads human innovators to these solutions is governed by trial-and-error. Even highly
11 prolific inventors testify to its importance. Among them is Thomas Edison, perhaps the
12 most prolific and certainly the most quotable on this subject. He tested “no fewer than
13 6,000 vegetable growths” as filaments for his first incandescent light bulb before he
14 finally stumbled on bamboo as the best material– temporarily, as it would later be
15 replaced by tungsten. He only slightly exaggerated the number of trials his inventions
16 require when he observed, “I have not failed. I have just found ten-thousand ways that do
17 not work.” (Alfred 2009) Decades later, John Backus, one of the creators of the computer
18 programming language FORTRAN echoed Edison when he said “you need the
19 willingness to fail all the time. You have to generate many ideas and then you have to
20 work very hard only to discover that they don't work. And you keep doing that over and
21 over until you find one that does work.” (Lohr 2007)

22
23 Some trial-and-error exploration of new technology has a methodical flavor. It considers
24 a specific problem and varies one or more parameters of candidate solutions to it. Such
25 parametric study was central to the invention of high-speed tool steel by Frederick
26 Winslow Taylor, who tested thousands of alloys using manganese, tungsten, and
27 chromium, at hundreds of different annealing, heating, and cooling temperatures (Kanigel
28 2005). The “father of civil engineering,” John Smeaton, demonstrated the improved
29 performance for undershot water wheels – wheels in which the water flows through the
30 bottom of the wheel, rather than over its top – in one of the most systematic parametric
31 experiments ever (Rosen 2010). The Wright Brothers developed the wing that would be

1 essential to the first airplanes by parametric variation of forty-eight different surfaces at
2 fourteen different angles in their Ohio wind tunnel (Tobin 2004).

3
4 Parametric testing is important, but we would be flattering ourselves if we thought this
5 relatively rational process was the main driver behind human innovations. Multiple key
6 innovations in the history of technology were as close to pure accidents as could be
7 imagined. One such accident led Thomas Newcomen's discovery of the atmospheric
8 steam engine. It occurred when a poorly soldered seam in an engine's outer envelope
9 broke, and accidentally injected a jet of cold water into the engine's steam cylinder,
10 condensing the steam immediately. Since condensed steam – water – takes up less than
11 1/10th of one percent of the space needed by steam, this leak turned the cylinder into a
12 vacuum chamber which exerted a huge amount of force on the engine's piston, and thus
13 demonstrated the principle of a working steam engine (Rosen 2010). Vulcanized rubber,
14 able to retain its flexibility in a wide range of temperatures, was discovered when Charles
15 Goodyear inadvertently dropped a compound of natural rubber, white lead, and sulfur on
16 a hot stove (Slack 2002), and the world's best-known nonstick substance was discovered
17 when a freezing experiment spontaneously turned a potential refrigerant gas into Teflon
18 (Plunkett 1986).

19
20 The immediate goal of an invention may be clearer to a technologist than it is to nature's
21 blind watchmaker (Dawkins 1986). However, such foresight usually does not extend far,
22 because even visionary inventors often fail to anticipate the ultimate use of their
23 discoveries. Wireless radio was invented by Guglielmo Marconi specifically for two-way
24 communication, and his company rejected the proposal to use the technology for
25 broadcasting news and entertainment, even though the idea came from one of their own
26 telegraphers, David Sarnoff, who would later found RCA (Bilby 1986). Edison at first
27 viewed his phonograph primarily as a tool for business communication (Stross 2007), and
28 while penicillin, as is well-known, was accidentally discovered through a contaminated
29 petri dish left out on a laboratory bench by the physician Alexander Fleming in 1928, it
30 was more than ten years before he or anyone else realized its potential as a revolutionary

1 medical treatment (Lax 2004). Examples like these remind us that we overestimate our
2 capacity for foresight.

3
4 A corollary to the importance of trial-and-error is that both biological and technological
5 evolution rely not on individuals but on populations. In biology this was first fully
6 realized early in the 20th century during the birth of population genetics, the discipline
7 that aims to describe how new variants of genes and genomes spread through
8 populations. Although highly mathematical, some of its principles are quite intuitive:
9 Because evolution proceeds by trial and error, large populations experience more trials,
10 and thus have a greater chance to draw the winning lottery ticket. And even though the
11 myth of the lone inventor is firmly lodged in the public imagination, technological
12 innovation relies on a similar principle. Edison's lighting experiments depended on a
13 staff of dozens of assistants, so much so that one of them, Francis Jehl, said that "Edison
14 is in reality a collective noun" (Kelley 2001). The importance of populations – from
15 collaborating groups to competing teams – has only increased since Edison's time and is
16 responsible for innovations as different as children's car seats and handheld computers
17 (Kelley 2001).

18 19 20 2. Extinction & Replacement

21
22 The nearly four-billion year long history of life can be viewed largely as a history of
23 species extinction – the flip-side of innovation. As many as 99.9% of all species that
24 emerged since life's origins are extinct today, together with the novel survival strategies
25 they once embodied (Raup 1991). Species extinction is a constant drizzle that is
26 sometimes punctuated by tropical downpours: mass extinctions that can kill more than
27 half of all species in one fell swoop. And phenomenal success, over periods of hundreds
28 of millions of years or more, offers no immunity. Sixty-five million years ago, the giant
29 dinosaurs, along with three-quarters of all other species, vanished in a geologic eye blink,
30 perhaps a few tens of thousands of years (Archibald & Fastovsky 2007). Their
31 disappearance 65 million years ago repeated the experience of most other form that

1 preceded them, such as the trilobites, ancient arthropods that filled the oceans until their
2 extinction some 250 million years ago.

3
4 The history of science and technology is impossibly brief compared to the four billion
5 years of life's history, but it already has its dinosaurs, even though technological
6 extinctions are more likely to be caused by competition rather than by huge extrinsic
7 events such as asteroid impacts. Obsolete technologies, from the stone ax to the horse
8 drawn carriage and the steam engine, litter technology's battlefields. And so do outmoded
9 scientific theories, such as Ptolemy's epicycles that allowed earth to remain at the center
10 of the solar system, or the Phlogiston theory of the 17th century. The best explanation of
11 phenomena like combustion and oxidation for nearly a hundred years, it was made
12 obsolete by the work of Antoine Lavoisier and the discovery of oxygen (Leicester &
13 Klickstein 1963).

14
15 Extinction is not always final, as successful resurrections in nature and technology
16 demonstrate. Amateurs of medieval coats of arms, steam engines, or vacuum tube
17 televisions have brought these technologies back to life. Thousands of enthusiasts have
18 revived the market for old-fashioned vinyl records, while others delight in loading and
19 firing black powder firearms. Such resurrection is only possible if the information needed
20 build an artifact or an organism is still available. From one perspective, human
21 technology is superior to nature in this respect, thanks to humans' extensive record
22 keeping, for example through patent applications. In contrast, life's records are written in
23 fossils that often do not preserve much more than the shape of an organism, and certainly
24 not the information in its DNA. Arguably, however, this comparison is not fair, given
25 life's long history: Would humans alive 100 million years from now be able to resurrect
26 our current technologies? What's more, resurrections of some organisms are eminently
27 feasible, such as the recently revived bacterium *Herminiimonas glaciei*, frozen three
28 kilometers below the surface of Greenland's ice sheet for 120000 years (Loveland-Curtze
29 et al. 2009). And while the dinosaur-reconstruction fantasy of the movie Jurassic Park
30 may remain science fiction forever, DNA molecules can already help reconstruct
31 complex *parts* of our long-extinct ancestors. A case in point is the 450 million year-old

1 ancestor of two different kinds of hormone receptors, the mineralocorticoid receptor and
2 the glucocorticoid receptor. Computational reconstruction followed by synthesis of the
3 ancestral protein from information in today's receptors showed that it was able to interact
4 with both hormones, and demonstrated how subsequent changes allowed it to specialize
5 on one of them (Ortlund et al. 2007). Unlike many technologies, organisms alive today
6 carry an extensive record of their extinct ancestry, most of it through ancient genes that
7 continue to serve the organism, some of it through defunct genes that can persist in a
8 genome for millions of years (Marshall et al. 1994). We have an "inner fish" (Shubin
9 2009), but a LED has no "inner candle". This inner record of life may ultimately provide
10 biologists with a great advantage in bringing back innovations from the dead.

11 12 3. Descent with Modification

13
14 The best-known instance of this principle in biology is the inheritance of mutationally
15 modified DNA from parents to offspring – "vertical" transfer across generations (as
16 opposed to the "horizontal" transfer discussed below). But it is not the only one instance:
17 In many animals, simple "technologies" like the sticks that help New Caledonian crows
18 forage and the marine sponges that help bottlenose dolphins hunt fish are passed from
19 generation to generation at least partly through social learning (Kenward et al. 2006;
20 Krutzen et al. 2005). Such cultural inheritance is a hint that descent with modification
21 may be just as important in the evolution of technology. And indeed it is. Archaeologists
22 successfully use Darwinian concepts to understand the material record of prehistoric
23 human cultures. For example, the tools of cladistics – a discipline that reconstructs
24 evolutionary history from patterns of inheritance with modification – has been used to
25 construct a phylogeny of the many forms of fluted points used in projectile weapons,
26 such as arrowheads and spear points, of Paleo-Indian cultures (O'Brien et al. 2001). A
27 recent study of more than one hundred separate design traits found in Polynesian canoes,
28 including the shape of the outrigger boom, the fibers used for lashing attachments
29 together, as well as the length and depth of the keel and ribs, identified a clear pattern of
30 descent by modification (Rogers & Ehrlich 2008). The table fork first appeared in Europe
31 in the early 14th century in a two-tined version, was slowly supplanted by one with three

1 tines, and then, in the 17th century, by a four-tined fork, which hasn't changed
2 substantially since (Petroski 1992). And 20th century innovation is also essentially a
3 litany of descent with modification. Examples include cars (Ford's Model T to the Prius),
4 planes (the Wright's brother's Flyer to the Boeing 787), and programming languages like
5 FORTRAN, which radiated into multiple different successor languages, such as Algol,
6 BASIC, and Python (Sole et al. 2013).

7 8 4. Horizontal Information Transfer 9

10 The cornet is a 19th century brass wind instrument that uses valves to produce different
11 notes by changing the shape of a vibrating chamber. Its history illustrates that descent
12 with modification is augmented by a form of horizontal transfer between
13 contemporaneous innovators. The reason is that two different valve systems – the Stölzel
14 and Périnet systems – were developed over time via such information transfer. When one
15 designer shifted valve location and alignment, or the placement and shape of the bell, the
16 other recognized the innovation, and incorporated it. The Stölzel valve, one hollow
17 cylinder inside another, appeared first, in 1825. It controlled airflow by admitting the air
18 along its longitudinal axis. About 1840, the Périnet valve “solved” the same problem by
19 controlling the airflow across its width. The Périnet valve did not just derive from its
20 “ancestor”, but was a solution that also depended on horizontal information transfer
21 (Eldredge 2011; Temkin & Eldredge 2007).

22
23 At least since the invention of written information transmission, knowledge has been
24 traveling between individuals and groups at an accelerating pace, thus facilitating such
25 transfer. Examples old and new abound, from gunpowder, which was invented in China
26 in the 9th century and spread from there (Needham 1954), to horses, which were
27 introduced to the New World by the Spanish conquistadores and eventually helped turn
28 North American Indians into the fearsome warriors that held expanding European
29 settlements in check for decades (Gwynne 2010). They also include post-industrial
30 technologies like – once again – programming languages, in whose radiation horizontal

1 transfer of language elements play a role, such as in the creation of BASIC, which
2 combined elements of Fortran and Algol (Sole et al. 2013).

3
4 Horizontal transfer is not a feature that that sets technological innovation apart from
5 nature's innovation. To argue otherwise is to ignore a key mode of innovation in the most
6 populous and prolific organisms on the planet: bacteria. The information they exchange
7 comes in the form of genes, which can get transferred through viruses, through a cell's
8 uptake of naked nucleic acids from the environment, or through a primitive form of sex
9 called bacterial conjugation (Bushman 2002; Horie et al. 2010). Such horizontal gene
10 transfer can alter genomes on short evolutionary time scales (Choi & Kim 2007; Daubin
11 & Ochman 2004; Lerat et al. 2005; Nelson et al. 1999; Ochman et al. 2000; Pal et al.
12 2005) . For example, it adds DNA to the *E. coli* genome at a rate of more than 60 genes
13 per million years (Blattner et al. 1997; Lawrence & Ochman 1998). Even closely related
14 strains of a bacterium like *E. coli* can differ in more than 20% of their genome, and may
15 have more than 100 added genes relative to other strains (Ochman et al. 2000; Pal et al.
16 2005). Horizontal gene transfer is so prevalent in bacteria that their evolutionary
17 relationships may not resemble so much a tree than a network, where the lineage of any
18 one species is a mosaic of different genetic influences (Doolittle 1999). And most
19 importantly, horizontal gene transfer is responsible for a wide variety of bacterial
20 innovations, such as the ability to digest and degrade toxic molecules, the ability to cause
21 infectious diseases, as well as the rapid spreading of antibiotic resistance through
22 worldwide bacterial populations (Bushman 2002). While rampant in bacteria, such
23 transfer has also been observed in other organisms, such as between yeast and fruit flies
24 (Li 1997). In general, however, horizontal transfer becomes rarer in distantly related
25 organisms (Thomas & Nielsen 2005; Wagner & de la Chaux 2008), which provides
26 another parallel to technological change, where the diffusion of innovations and ideas is
27 far more frequent *within* societies, and especially within those that share a scholarly
28 tongue – medieval Europe, or Islam, or China – than between them (Mokyr 1990).

29
30 The boundaries between descent by modification and horizontal transfer are not clean-
31 cut, which is obvious in technological change, but just as true in biology. The best

illustration is sexual reproduction in organisms like us. It involves a form of horizontal transfer that shuffles genetic information between two organisms in the same population, but this shuffling always leads to reproduction – vertical descent. This stands in contrast to bacterial sex, where horizontal exchange is independent from vertical information transmission. The power of mixing vertical descent with horizontal exchange is best illustrated by its prevalence in higher organisms. With few exceptions, lineages without the ability to reproduce sexually are evolutionary dead ends. Most of them have only emerged recently in evolution and do not persist for long. Creating new variation is one of several reasons for this prevalence of sex (Futuyma 2009, Ch. 15).

5. Combinatorial innovation

The importance of horizontal gene transfer foreshadows our next principle, namely that innovation frequently results from assembling what already exists into new combinations – re-combination, in the most general sense of the word.

Consider pentachlorophenol, a highly toxic man-made molecule introduced in the early 20th century, used as an insecticide, fungicide, and disinfectant. Some organisms, such as the aptly named bacterium *Sphingobium chlorophenolicum* thrive on it, using pentachlorophenol as their only source of energy and carbon. This bacterium converts pentachlorophenol into a less toxic molecule that it can feed on, with the aid of four chemical reactions that are catalyzed by enzymes and encoded by genes. Individually, these reactions occur in many other organisms, where they help recycle superfluous amino acids in some, and disarm various toxic molecules in others. The innovation of *S. chlorophenolicum* – brought about by horizontal gene transfer – lies in the new *combination* of these enzyme-catalyzed reactions. Similar recombination also occurs in other metabolic innovations, such as the urea cycle of land-living organisms, a once-novel cycle of five enzyme-catalyzed chemical reactions that helps them detoxify ammonium waste and excrete it in their urine as urea. The individual reactions are widespread in other organisms, and help manufacture or recycle amino acids. What is novel is their combination (Takiguchi et al. 1989).

1
2 Perhaps the clearest illustration that innovation in nature is combinatorial comes from the
3 biological macromolecules ribonucleic acid (RNA) and proteins. Each of these polymers
4 is a string of simpler building blocks – four different nucleotides in the case of RNA, and
5 twenty amino acids in proteins – that play thousands of different roles in the life of any
6 organism, from regulation to transport, communication, and catalysis. All of these
7 functions arose by changing the individual nucleotide sequence of an RNA or protein
8 molecule. Put differently, new molecules of this kind are simply new combinations of a
9 few chemical “letters”.

10
11 The most familiar analogy to this process is cultural: The same twenty-six letters, plus a
12 few punctuation marks, can be reshuffled to produce *Great Expectations* or *The Great*
13 *Gatsby*. But technological innovation is also combinatorial in less obvious ways. A
14 typical and much cited example is the jet engine that transformed aviation in the middle
15 of the last century (Arthur 2009). It consists of three components, a compressor, a
16 combustion chamber, and a rotating turbine. Each of them has a long history of functions
17 unrelated to generating thrust. Compressors, in the form of bellows, had been a core
18 technology for blacksmiths for more than 2000 years. Combustion chambers are essential
19 for the internal combustion engines of automobiles. And the precursors of screw turbines
20 have existed since Archimedes. The power of combinatorial innovation is just as
21 apparent in less complex technological innovations. The bench vise, for example, is a
22 powerful 18th century combination of two simple machines that date to antiquity, a lever
23 and a screw. The front-mounted wheelbarrow, which first appeared in Europe in the 12th
24 century, combines the mechanism of a lever with that of a wheel (Lewis 1994). Newer
25 but just as useful is the adjustable wrench, which combines the mechanical advantage of
26 a lever with that of a screw.

27
28 The insight that combinatorial innovation pervades technology just as it pervades nature
29 is not recent. When the economist Brian Arthur states that “technologies somehow must
30 come into being as fresh combinations of what already exists” (Arthur 2009) he is
31 extending the ideas of the economist Joseph Schumpeter who defined entrepreneurship as

1 the creative recombination of existing ideas (Schumpeter 1989). Another economist, Joel
2 Mokyr, has argued that a new technological process – a “technique” in his formulation –
3 appears when the knowledge underlying two different techniques are joined in a novel
4 fashion (Mokyr 2000).

5 6 6. Exaptation

7
8 The ubiquity of combinatorial innovation has a corollary. In an innovation, the parts of a
9 biological or technological system are often co-opted for new purposes unrelated to the
10 reasons for their origin. In biology, this phenomenon was known to Charles Darwin more
11 than a hundred years before the late paleontologist Stephen Jay Gould christened it
12 *exaptation* (Gould & Vrba 1982). Darwin reminded readers of the *Origin of Species* that
13 “an organ originally constructed for one purpose...may be converted into one for a widely
14 different purpose...” (Darwin 1872, p 175), using examples like the transformation of
15 flotation bladders of fishes into the lungs of terrestrial animals. Thousands of others
16 examples known today include the feathers of birds, which originated most likely to
17 insulate or waterproof a body, and were only later “exapted” for flying (Sumida &
18 Brochu 2000). Made especially famous by an eponymous essay of Gould (Gould 1980) is
19 the Panda’s “thumb”, an extra digit that helps this herbivore strip leaves from bamboo
20 stalks, the better to eat only the shoots. Because the Panda’s forearms also have five
21 regular digits, this thumb cannot share a common ancestry with our thumb. It happens to
22 be a greatly enlarged wristbone, equipped with muscles and co-opted for a new use.

23
24 Exaptations permeate life down to the level of molecules. One exapted molecule is
25 lysozyme, an enzyme that helps organisms defend themselves against bacteria by killing
26 them. This enzyme has been co-opted in mammals to help them synthesize lactose, a
27 prominent sugar in mammalian milk (McKenzie & White 1991). Another example is a
28 protein called “Sonic hedgehog”, which helps sculpt fingers and the spinal chord in our
29 bodies, but molds feathers in birds (McKenzie & White 1991). Such molecular
30 exaptations illustrate that some innovations can originate as mere by-products of
31 evolution, for no adaptive reason at all. Examples include hundreds of promiscuous

1 enzymes, so-called because they catalyze a main chemical reaction that is important to an
2 organism's survival or reproduction, but also also a spectrum of side reactions that can
3 later become adaptations (Aharoni et al. 2005; Nam et al. 2012; O'Brien & Herschlag
4 1999). At least as abundant are insertions of transposable elements – mobile pieces of
5 DNA that can change location within a genome – near a gene. They often happen to carry
6 stretches of DNA that can activate the nearby gene, which is often inconsequential at first
7 but can come to provide a benefit later (Santangelo et al. 2007).

8
9 Exaptation is no less ubiquitous in technology than in nature. A classical example is
10 Johannes Gutenberg's printing press, which, in the words of Stephen Johnson "borrowed
11 a machine designed to get people drunk" – a screw-driven wine-press – "and turned it
12 into an engine of mass communication." (Johnson 2010). Microwave ovens heat food
13 with a technology originally developed for radar – the first commercial version was
14 called the "Radarange" (Murray 1958). The powerful and quick-acting cyanoacrylate
15 adhesive marketed as "Loctite," "Super Glue," and "Krazy Glue" was discovered by
16 researchers at Eastman Kodak working on plastic gun sights for WWII combat aircraft
17 (Harris 2011). Once one accepts the combinatorial nature of both kinds of innovation, the
18 importance of exaptation in both nature and technology comes as little surprise.

19 20 21 7. Ecosystem engineering

22
23 A beaver that builds a dam and a lodge creates not only shelter from wolves and other
24 predators through impenetrable mud walls, easy access to food through underwater
25 entrances, and a dry den to raise its family. It also engineers an entire ecosystem. Beaver
26 dams restore wetlands that can nurse many species, such as salmon and frogs, provide
27 flood control, and nourish bacteria that feed on decaying cellulose and absorb excess
28 nutrients such as phosphates and nitrates.

29
30 Organisms that engineer ecosystems, a process also known as niche construction,
31 transform their environment, whether actively like the beaver or passively through their

1 mere presence. And such organisms are legion. They include the more than 10,000
2 species of nest-building ants and termites. They also include the trees in terrestrial
3 forests, which change the cycling of water and thus affect the weather experienced by all
4 organisms around them. And they include microbes such as oral bacteria that secrete
5 sticky polymers to form biofilms that protect them from the assault of toothbrushes, and
6 marine phytoplankton that can increase ocean surface temperatures through light
7 absorption and scattering (Day et al. 2003; Jones et al. 1994).

8
9 The most important point about ecosystem engineering is not that it creates new
10 environments, but that these environments can guide future innovations.
11 Some frogs and reptiles that construct their niches through burrowing have evolved
12 specialized limbs and hardened snouts to help them do so. Ants not only build nests, they
13 also have evolved the ability to regulate a nest's temperature by plugging holes to prevent
14 heat loss, or by adjusting a mound's slope to change heat absorption from the sun. Some
15 burrowing spiders can equip their surroundings with silken trip wires to alert them to a
16 prey's approach. Weaverbirds first evolved the ability to build simple nests, and only
17 later the skill to elaborate these structures, such as by building roofs to keep their chicks
18 dry.

19
20 Radically new kinds of niches – their origins go back to life's earliest times – even create
21 platforms for change that can give rise to entirely new forms of life. The evolution of
22 photosynthesis transformed our atmosphere from a mix of toxic gases to its present
23 oxygen-filled state, which made the life of animals and humans possible in the first place.
24 A bit later, the conquest of land by animals created a new platform – literally – for
25 terrestrial life, on which organisms as diverse as dinosaurs, birds, and mammals arose.

26
27 The technological innovations of humans also transform the environment, with numerous
28 parallels to ecosystem engineering in nature. For example, Jones and collaborators write
29 in a review on ecosystems engineering that “from a functional perspective we see no
30 difference between human and non-human engineering” (Jones et al. 1994, p 379). And
31 like in nature, new technologies create new niches (Nelson & Winter 1977), platforms for

1 future innovations. This has been the case throughout the history of technological
2 evolution, whose key moments Schot and Geels define as “the establishment of a new
3 sociotechnical regime,” that is, any change that transforms the way people interact with
4 technology (Schot & Geels 2007).

5
6 Examples include the wheeled moldboard plow, which first appeared in Europe
7 during the Middle Ages, allowed the cultivation of heavy soils, and thus enabled the
8 production of enough cereal grains to feed the continent’s growing population (White
9 1966). That increased population, in turn, required the deforestation of millions of acres
10 to produce more arable land, an activity that demanded innovations in the blast furnaces
11 and forges that manufactured iron axes for an entire continent (Williams 2006). More
12 iron meant fewer trees, until the 18th century, when the scarcity of charcoal fostered yet
13 another innovation, the use of the purified charcoal known as coke. This is the fuel that
14 not only smelted the iron for the Industrial Revolution’s locomotives, but ran them as
15 well (Ferguson 1967).

16
17 As on land, so at sea. In the 10th century, Viking long ships connected the Old World and
18 the New for the first time, using the technological innovation known as a sun-compass, a
19 circular sundial with an adjustable gnomon whose shadow would hit a particular spot on
20 the circle at noon, indicating the ship’s latitude, and so allowing dead reckoning
21 (Ferguson 2009). As the technology of sailing improved, the range of potential trading
22 and raiding expeditions improved with them, demanding still more technological
23 improvements, as the sun-compass gave way to the mariner’s astrolabe, followed
24 successively by the backstaff, the octant, and the sextant, each one an innovation in
25 navigation required for voyaging farther and farther from land (Taylor 1971).

26 27 8. Episodic Change

28
29 In addition to the commonalities that we already encountered, biological and
30 technological innovations also share a similar rhythm. In both spheres, the rate at which
31 innovations appear is not smooth and regular, but sharply episodic.

1
2 Ever since Darwin himself, biologists have been puzzled by the scarcity of fossils that
3 document transitions to major innovations, despite exceptions such as Archeopteryx,
4 which marks a transition between dinosaurs and birds, Tiktaalik, a more than 350 million
5 year old four-limbed fish (Daeschler et al. 2006), or Runcaria, a precursor of a seed-
6 bearing plants (Gerrienne et al. 2004). The rarity of such transition fossils cannot always
7 be explained away by an incomplete fossil record, as generations of paleontologists
8 chipping away at Nature's secrets have learned. Nature's motto seems to be "hurry up and
9 wait". In many lineages, little change is happening most of the time and when change
10 happens, it happens rapidly. Such stasis, interrupted by rapid, punctuated change is well-
11 documented in some bryozoans ("moss animals"), small plant-like marine animals that
12 form colonies by budding-off small "zooids". Some fossil American bryozoans persist
13 virtually unchanged for up to 16 million years, only to give abruptly rise to new species
14 in a blink of the geological eye (Eldredge et al. 2005; Jackson & Cheetham 1999). In
15 some trilobites, eye architecture remains unchanged for long time intervals, only to
16 change abruptly after such a period of stasis (Futuyma 1998 Ch. 6). The most dramatic
17 example of such punctuated change is the Cambrian explosion itself, a short period of
18 geological time more than 500 million years ago that brought forth all major animal
19 groups alive today (Futuyma 1998 Ch. 7).

20
21 The history of technological evolution displays a very similar pattern of episodic change,
22 with long periods of relative stagnation punctuated by periods of major change like the
23 Industrial Revolution. Such bursts of innovation are often characterized by singular
24 "macroinventions," dramatic leaps of innovation like the first atmospheric steam engine
25 that are by definition rare. Perhaps the most significant example of technological
26 stability punctuated by episodic change is the technology of information transfer.
27 Kilgour, in *The Evolution of the Book*, cites only four significant innovations in the entire
28 history of written communication: The clay tablet of 2500 BCE, the papyrus roll/scroll
29 of 2000 BCE, and the codex (i.e., the modern leaved book) around 150 CE, which has
30 been virtually unchanged until the advent of the e-book around 2000 BCE (Kilgour
31 1998).

Macroinventions are to technology what the evolutionary leaps that the 20th century geneticist Richard Goldschmidt called “hopeful monsters” – dramatically changed organisms that are not necessarily improvements (Chouard 2010; Theissen 2006). There is no gradual movement from semaphore to electrical telegraph, or from telegraph to the first radio transmission by Marconi, or from transmissions that used relatively long electromagnetic waves (>1000 m) to shortwave (<200 m) transmissions) (Mokyr 1990). Such macroinventions are complemented by microinventions, incremental improvements in existing technologies analogous to the gradual adaptation typical of biological evolution, which can either precipitate or follow macroinventions. The slow accumulation of small technological changes can cause a tipping point towards a giant improvement, such as in the e-book reader, the most recent macroinvention of reading technology. It was facilitated by dozens of microinventions, from the development of hypertext at Stanford Research Institute in the 1960s (Bardini 2000) to electronic paper displays, invented at MIT in the 1990s (Jacobson & Comiskey 1999). Conversely, macroinventions can also enable microinventions. In Kilgour’s example, the printed codex was successively improved by printing with moveable type by Gutenberg in 1450, by steam power in the 19th century, and by offset printing in 1970 (Kilgour 1998).

9. Multiples and Singletons

Breakthroughs in science and technology may be rare, but history documents numerous occasions in which they appeared more than once, and independently from each other. Already in the 1920s, William F. Ogburn and Dorothy S. Thomas compiled more than 100 cases of independent discovery and invention (Ogburn & Thomas 1922). The sociologist Robert K. Merton built on their work in the 1960s and called such discoveries “multiples” (Merton 1936; Merton 1968). Notable examples in science include the virtually simultaneous formulation of calculus by Newton and Leibniz, and of logarithms by Joost Bürgi and John Napier. The physical law that holds a gas’s pressure inversely proportional to its volume is known as Boyle’s Law in most of the world, but as Mariotte’s Law in Francophone countries, respectively for Robert Boyle and Edme

1 Mariotte, who discovered it independently. The father of the Hungarian mathematician
2 János Bolyai, who formulated non-Euclidean geometry at the same time as the Russian
3 Nikolai Lobachevsky, observed, “mathematical discoveries, like springtime violets in the
4 woods, have their season which no human can hasten or retard” (cited in (Kleiner 1988)).
5 Even the theory of evolution by natural selection was famously formulated
6 simultaneously and independently by both Darwin and Alfred Russel Wallace. And
7 likewise for new technologies. The world’s first practical steamboats were independently
8 invented by the Americans Robert Fulton and James Rumsey and the Marquis de
9 Jouffroy, a French aristocrat (Rosen 2010). Elisha Gray and Alexander Graham Bell
10 filed for a patent on a working telephone on the same day in 1876 (Ogburn & Thomas
11 1922). Patents for incandescent light bulbs were granted more than twenty different
12 times before Edison (Sole et al. 2013).

13
14 Multiple origins also abound in biological innovation, although not necessarily with near-
15 simultaneity. Perhaps the best known examples of such *convergent* traits are lens-
16 equipped eyes in vertebrates and in the octopus, and in the wings of insects and birds.
17 They have plenty of company. In a 2006 paper, the paleontologist Geerat Vermeij listed
18 more than 50 innovations with independent origins, as different as the leaves of plants,
19 which originated both in land plants and in aquatic plants like algae, the production of
20 silk in spiders and silk moths, and the electrosensory organs of African and South
21 American fish (Vermeij 2006). And once again, convergent origins occur on all levels of
22 the biological hierarchy, down to the molecular level. Take the innovation that solved a
23 crucial problem of early life, how to extract carbon – a key building material for cells and
24 organisms – from carbon dioxide in the air. The best-known solution is that of plants,
25 which use the energy of sunlight and an enzyme called RuBisCo (Ribulose-1,5-
26 bisphosphate carboxylase oxygenase) to attach carbon dioxide to a sugar which is then
27 incorporated into biomass. But this solution is not the only one. Some microbes attach
28 carbon dioxide to the carrier molecule acetyl-CoA, yet others add it to molecules from
29 the ancient citric acid cycle (Rothschild 2008).

1 Molecular examples like this one also show that independently discovered solutions are
2 often different from one another. Organisms can detect light waves using either a flexible
3 single lens like ours, or the rigid compound eye of a fly. Crystallins, the transparent
4 proteins in eye lenses that help us, other vertebrates, and molluscs create sharp images on
5 the retina originated from enzymes, but from enzymes with different function and
6 structure (Cheng 2006; Cheng 1998; Piatigorsky & Wistow 1989). And antifreeze
7 proteins have originated independently in Arctic and Antarctic fish, from ancestral
8 proteins with different functions (Cheng 2006; Cheng 1998).

9
10 Other innovations are what Merton called singletons (Merton 1961) which occur either
11 because a problem has only a single solution, or as the result of what the biologist Francis
12 Crick termed a “frozen accident” (Crick 1968): One among multiple potential solutions
13 that happened to be discovered first, and prevents the adoption of later and perhaps
14 superior solutions through the self-explanatory *first mover advantage* (Lieberman &
15 Montgomery 1988). Aside from the most familiar QWERTY keyboard, which is not
16 demonstrably superior to other layouts (Leibowitz & Margolis 1990; Mayo et al. 2007),
17 the “Audion” vacuum tube patented by Lee de Forest in 1908 also falls into this category.
18 It became the standard for early radio, though technologies based on the oscillating arc or
19 the frequency alternator could have served just as well (Mokyr 2000). In a similar vein,
20 the world’s standard railway gauge, used today on more than 60% of all railroads and
21 virtually all high-speed lines – 4 feet, 8½ inches – is the same as the one used for the
22 horse-drawn rails at Killingworth Colliery in 1814, when the engineer George
23 Stephenson used them for his experimental locomotive (Puffert 2009; Rosen 2010).

24
25 We cannot be certain whether singletons in biology are truly frozen accidents or superior
26 choices (Vermeij 2006), but some candidates for frozen accidents do exist. Most
27 biological processes use only one of two or more mirror-symmetric, but otherwise
28 completely equivalent, forms of the same molecule (Siegel 1998). Our bodies use
29 adenosine triphosphate (ATP) as a universal energy currency, though related molecules
30 like guanosine triphosphate (GTP) could do the same job. Another candidate for a frozen
31 accident is the inverted organization of our retina, which is demonstrably *inferior* to

alternatives such as that of the squid's eye: Our light-sensing cells are removed from the light-exposed surface by layers of blood vessels and nerve cells, whereas these cells are on top in the squid's retina, closest to the light (Schwab 2012).

10. Spaces of the possible

Most commonalities between innovation in nature and technology need little explanation. Trial and error in populations become self-evident necessities, once we accept that humans – like nature – are very poor at anticipating successful innovations. Similarly, extinction results inevitably from limited space and resources in both the natural and technological world. Vertical and horizontal transfer of information are the only two principal modes by which one could tinker with the old in order to create the new (Jacob 1977). And such tinkering is inevitable in a non-creationist world, where the new does not emerge in perfection.

The reasons behind other commonalities are less obvious, but in biology a framework has emerged that can help explain them, and that is relevant for technological innovation. We will illustrate it with proteins, a specific class of systems involved in many innovations, but it applies also to all other systems known to be involved in molecular and macroscopic biological innovations (Wagner 2011).

At each position of the amino acid string that constitutes a protein, one of 20 different kinds of amino acids can appear. There are $20^{100} \approx 10^{130}$ such strings for proteins that are 100 amino acids long. Fewer than 20 kinds of amino acids may suffice to create proteins with most functions (Dryden et al. 2008), but because proteins can be thousands of amino acids long, it is safe to say that the space of possible proteins – of amino acid sequences or protein *genotypes* (Maynard-Smith 1970) – is enormous. Inside an organism, most proteins fold in three dimensions through thermal motion, and this *fold*, which constantly wiggles and vibrates, is responsible for what a protein can do, its *phenotype* and function (Branden & Tooze 1999). Since protein genotype space comprises all possible proteins, it

1 also comprises proteins with all possible functions, and thus all possible innovations that
2 involve proteins.

3
4 The very existence of such a space already helps explain the combinatorial nature of
5 innovation and the ubiquity of exaptation. Both emerge very naturally from the
6 realization that new proteins are new combinations of old amino acids, and such
7 combinations almost inevitably provide new uses for the old, and thus create the potential
8 for exaptation. What is more, because the framework of genotype space applies to
9 innovations beyond new proteins – involving novel forms of regulation or of metabolisms
10 – it can help explain the combinatorial nature of all biological innovation (Wagner 2011).

11
12 To understand Merton's multiples in biology, one needs to go beyond the mere existence
13 of genotypes spaces and understand their internal organization. This organization is
14 highly peculiar, and shared among different kinds of genotype spaces (Wagner 2011).
15 Specifically, any one phenotype is usually formed by astronomically many different
16 genotypes, e.g., there are myriad different amino acid strings that have the same fold and
17 function. What is more, many of these genotypes form connected networks (Schuster et
18 al. 1994; Wagner 2011). In such a *genotype network*, the smallest possible change in a
19 genotype – the alteration of a single amino acid in a protein, for example – can lead to a
20 “neighboring” protein with the same phenotype. A series of further such changes can
21 transform the starting genotype, and create an amino acid string with little resemblance to
22 that of the starting protein, but – and this is important – through all this genotypic change,
23 the phenotype can remain unchanged. Merton's multiples are a consequence of this
24 organization. All the genotypes in a genotype network can be viewed as different
25 solutions to a given problem, such as how to catalyze a particular chemical reaction.
26 Through the haphazard way in which biological evolution explores genotype space, it is
27 apt to discover different solutions in different organisms, merely because so many
28 different solutions exist. (These networks have a straightforward relationship to fitness
29 landscapes (Svensson & Calsbeek 2012), a concept central to evolutionary biology where
30 genotypes are assigned different altitudes in a multidimensional landscape according to

1 their fitness: Genotype networks correspond to contour lines in such a landscape, formed
2 by genotypes with approximately equal fitness.)

3
4
5 Some innovations may be only a few mutations away from an already existing genotype,
6 but others may reside very far away in genotype space. To find them, many trials (and
7 errors) may be necessary. What's more, improving existing innovations can become more
8 and more difficult as these innovations approach perfection in any one environment.
9 Sometimes, further improvement is impossible unless the environment itself changes and
10 triggers opportunities for more innovation. Episodic evolution, where bursts of
11 innovation inevitably alternate with periods of stasis is, like the ubiquity of multiples, a
12 natural consequence of the vast size and organization of genotype space (Fontana &
13 Schuster 1998; Schuster 2003).

14
15 Technological systems share the very properties – multiples, combinatorial innovation,
16 etc. – that genotype spaces can explain in biology. This suggests that explaining these
17 commonalities requires analogs to genotype spaces in technology. Such an analog would
18 harbor all possible solutions to problems that can be tackled with a given technology.
19 One might call it a discovery or innovation space – it has also been called a design space
20 (Stankiewicz 2000) – because it contains all possible innovations that a technology
21 allows. Like the genotype space of proteins, it is a space of the possible.

22
23 The idea that technological innovation takes place in such a space is not a mainstream
24 notion, but neither is it new. It goes back at least to the “mechanical alphabet” of
25 machines proposed by the 18th century Swedish industrialist and inventor Christopher
26 Polhem (Strandh 1987). The letters in this alphabet are simple machine parts, including
27 wedges, screws, levers, and winches. Polhem believed that one could build any
28 mechanical device by combining these parts. In a similar vein, the art historian George
29 Hersey and computer specialist Richard Freedman searched for a way to characterize the
30 essence of buildings designed by the famed 16th century Venetian architect Andrea
31 Palladio (Hersey & Freedman 1992) and formulated a computer algorithm that can
32 generate thousands of different floor plans – all recognizably Palladian – based only on a

1 small number of simple rules that subdivide a rectangular building into smaller rooms.
2 More recently, Sanchez and Mahoney have pointed out that the automobile, aircraft,
3 consumer electronics and other industries build many different products by combining a
4 limited number of “modular” components (Sanchez & Mahoney 1996).

5
6 All human innovation takes place in some space of the possible, but human innovators do
7 not yet take advantage of this space in the way evolution does. For example, combining a
8 compressor, a combustion chamber, and a turbine into a jet engine (Arthur 2009) is
9 dependent on ingenuity – it is not obvious how to combine the elements of an existing
10 technology to innovate. The blind innovation process of nature compensates for its lack
11 of ingenuity by using components whose links are standardized, such that their
12 combination does not require ingenuity, but only patience. A case in point is the peptide
13 bond of proteins, a type of chemical bond that allows any two of the 20 proteinaceous
14 amino acids to connect to one another. It is this peptide bond that allows nature to explore
15 myriad different amino acid sequences. Other examples of standardized linkages include
16 that between regulatory proteins and the DNA words they bind, which help build and
17 alter gene regulation patterns, and, most fundamentally, DNA itself, whose nucleotides
18 are linked through the standardized phosphodiester bond, which allows mindless
19 exploration of myriad possible DNA strings, no ingenuity required.

20
21 Standardized linkage makes a systematic exploration of an innovation space possible.
22 And while we know about it mostly from nature, it is not beyond human technology, as
23 the example of digital logic circuits – the heart of digital computers – shows. Their power
24 lies in the wiring. In any one such circuit many logic gates, elementary units capable of
25 simple computation are wired together, and their specific wiring pattern allows them to
26 perform the complex computations that run devices from simple calculators to
27 smartphones to desktop computers to data warehouses and servers that maintain the entire
28 Internet (Balch 2003). Different wiring patterns of few gates can create an enormously
29 diverse family of circuits, and in some circuits this wiring can be changed while a circuit
30 is operating (Balch 2003).

1 Logic gates are analogous to amino acids, their (standardized) wiring is analogous to the
2 peptide bond, and the computation that this wiring allows is analogous to the fold and
3 function of a protein. Recent work has shown that a circuit space defined by all possible
4 wirings of a few logic gates, has an organization similar to those of protein space (Raman
5 & Wagner 2011a). And exploring this space in the trial-and-error way of biology would
6 reveal properties like Merton's multiples – circuits with different wiring but the same
7 function.

8
9 In sum, the organization of innovation spaces in biology can help us understand some of
10 the more mystifying commonalities between technology and biology. (If innovators have
11 not traditionally thought about innovation in these terms, it is because the organization of
12 an innovation space is not as clear-cut in most technologies as in the digital circuit
13 example.) And this organization may even help accelerate future innovation.

14 Evolutionary principles already do, in the field of evolutionary computation, which
15 develops powerful techniques that mimic evolution by mutation and selection, and that
16 can reproduce known innovations and create new ones, for example in electronics (Koza
17 1992; Mitchell 1998). However, technologists could take even better advantage of
18 nature's innovability, at least for technologies whose innovation spaces are like those of
19 nature. These will be technologies where few kinds of parts are connected in standardized
20 ways, and where multiple configurations of these parts can solve the same problems.

21
22 The points of correspondence between biology and technology we discussed are far from
23 complete (Johnson 2010; Sole et al. 2013; Vermeij & Leigh 2011). Yet they already
24 insinuate that highly successful biological and technological systems share a property that
25 is independent of both biology and technology. This property, one might call it
26 *innovability*, emerges from the organization of a space of possible innovations, designs,
27 or genotypes (Wagner 2011). Because such spaces are mathematical concepts, one could
28 easily dismiss them and their organization as figments of our imagination, were it not for
29 what Nobel laureate Eugene Wigner called the "unreasonable effectiveness of
30 mathematics" in explaining the natural world (Wigner 1960). It suggests that such spaces
31 and the innovations therein have an existence beyond our limited minds. And while

1 concepts like this, for more than two millennia, were the subject of non-experimental
2 disciplines like mathematics and philosophy, they have now become accessible to
3 experimental science. For example, recent technological advances in biology permit the
4 synthesis of arbitrary new protein genotypes. In doing so, they also permit the exploration
5 of a genotypes space through experiment and computation (Forster & Church 2007;
6 Hietpas et al. 2011; Purnick & Weiss 2009). Technological systems are not far behind, as
7 explorations of digital circuit spaces testify (Raman & Wagner 2011b; Thompson &
8 Layzell 2000). Efforts like this will undoubtedly accelerate the demolition of the
9 conceptual wall separating biological and technological innovation.

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